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The Larvae Of The Chrysomelidae.

THE LARVAE OF THE CHRYSOMELIDAE

BY

JOSEPH LYONEL KING

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THESIS

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June 2, 1916

I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPER-
VISION BY Joseph Lyonel King

ENTITLED The larvae of the Chrysomelidae

BE ACCEPTED AS FULFILLING THIS PART OF THE REQUIREMENTS FOR THE
DEGREE OF Master of Science

Alex. D. MacGillivray

In Charge of Thesis

Stephen A. Forbes

Head of Department

Recommendation concurred in:*

Committee

on

Final Examination*

*Required for doctor's degree but not for master's.

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TABLE OF CONTENTS

I	Introduction	1
	The Chrysomelidae	
	Previous Investigations	
	Economic Value	
	Taxonomic Value	
	Scope of Thesis	
	Acknowledgements	
II	The Morphology of the Larvae	6
III	Subfamily Chrysomelinae	7
	Leptinotarsa decemlineata	
	The Head	
	Fixed Parts	
	Movable Parts	
	The Thorax	
	The Thoracic Legs	
	The Abdomen	
IV	Subfamily Galerucinae	17
	Galeruca sp.	
	The Head	
	Fixed Parts	
	Movable Parts	
	The Thorax	
	The Thoracic Legs	

The Abdomen

Phyllobrotica discoidea

The Head

Fixed Parts

Movable Parts

The Thorax

The Thoracic Legs

The Abdomen

V Subfamily Halticinae

23

Dibolia borealis

The Head

Fixed Parts

Movable Parts

The Thorax

The Thoracic Legs

The Abdomen

VI Subfamily Cassidinae

26

Chelymorpha argus

The Head

Fixed Parts

Movable Parts

The Thorax

The Thoracic Legs

The Abdomen



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VII	Subfamily Chlamydinae	30
	<i>Chlamys plicata</i>	
	The Head	
	Fixed Parts	
	Movable Parts	
	The Thorax	
	The Thoracic Legs	
	The Abdomen	
VIII	Subfamily Donaciinae	35
	<i>Donacia</i> sp.	
	The Head	
	Fixed Parts	
	Movable Parts	
	The Thorax	
	The Thoracic Legs	
	The Abdomen	
IX	Bibliography	40
X	List of Abbreviations	41

I INTRODUCTION

The members of the order Coleoptera or beetles undergo a complete metamorphosis in their development. The eggs of beetles generally are of moderate size and commonly globular or elongate in form. Their larvae vary considerably in form, ranging from the campodeiform to the eruciform type. The pupae have their appendages free. The pupae are commonly formed within the larval burrows, or in cells in the soil or decaying wood, and in several families they are suspended from plants, and only in a few cases (they are) protected by silken cocoons. The adult insects of this order show considerable variation in form; however, they may be characterized by the possession of horny wing-covers or elytra, which meet in a straight line on the dorso-meson, and beneath which is a pair of membranous wings. In all stages the Coleoptera are mandibulate.

In the coleopterous family Chrysomelidae the adults may be recognized by their more or less oval form, their three-segmented labial palpi and by having the fourth tarsal segment inconspicuous and fused with the fifth. All the members of the groups feed upon plants. The eggs are usually elongate and yellowish in color. Generally they are deposited on the leaves and stems of the food plants. The larvae are commonly eruciform. They may be leaf-feeders, living exposed on the food plant, in which case they are more or less highly colored, or they may be leaf-miners, stem-borers, or root-feeder, in which case they are usually slender in form and white in color. In the Clythrininae

and Chlamydinae the larvae are case-bearers, constructing their cases of excrement and cast skins, and with the tortoise beetles the larvae mask themselves beneath shield-like coverings of the same material. The pupae may be formed suspended from the food plant or in earthen cells in the soil and in the Donaciinae they are formed in silken cocoons beneath the water on the roots of water-plants.

Previous Investigations. - At the present time entomological literature is rich in publications on the taxonomy and morphology of adult insects and one may safely say that practically all of our common insects may be quite easily classified if one has access to the literature. Strange as it may seem, there are no complete keys yet published which will enable the entomologist to identify even the orders of immature insects. There are several groups, however, which have been systematically treated by several writers. Among these may be mentioned the work of MacGillivray ^{(3)*} on the larvae of the Tenthredinoidea and Coleoptera, Needham ^{(5)*} on the Odonata, Fracker ^{(1)*} on the larvae of the Lepidoptera, Mosher ^{(4)*} on the pupae of Lepidoptera, Riley and Johannesen ^{(6)*} on the Diptera of medical importance, and Howard, Dyar and Knab ^{(2)*} on the Culicidae. As a general rule most of the work on immature stages has been stimulated through the great economic importance of the group under consideration. This is illustrated by the work on the culicid larvae, all of which developed after the discovery that

* Numbers refer to the bibliography, page 40.

mosquitoes were the transmitting agents and hosts of the yellow fever and malarial organisms. Most of the important insects injurious to agriculture have been worked upon and in many cases their immature stages are well known and have been described and figured. This work, however, is incomplete and of a fragmentary nature owing to its sporadic origin, and consequently it has not been possible to organize it for systematic study.

Economic Value. - From an economic point of view a systematic study of immature forms is of great importance, though little has been done. With most of the economic species the greater damage is done during the growing period of the insect's life and is consequently caused by the larvae. In many cases the economic entomologist, after finding the larvae of some insect feeding upon an important crop, is compelled to take time to rear the larvae to maturity in order to determine the species and the possible means of control. This in some cases may require only a few days but in most cases it would be a period of several weeks or months and in others a year or more. If, on the other hand, there were keys and literature on the immature forms, the species could be determined and control measures immediately decided upon long before the appearance of the first individual. .

Taxonomic Value. - The study of immature insects has a further bearing on our knowledge of the taxonomy and morphology of adult insects. A true classification of any group of animals should rest not only on a study of comparative morphology of the animals to be classified, but should include

as well a study of comparative embryology. In most of the zoological groups the classification is based on such evidence and often is strengthened by the support of paleontology. With the Hexapoda, the classification is founded on the comparative morphology of the adult, no attention being given to the immature stages beyond the usual subdivision of the class into orders with a complete or incomplete metamorphosis. The necessity for a knowledge of larval forms is well illustrated in a number of instances where dimorphism occurs to such an extent that individuals of the same species have been considered as separate and distinct species. This is illustrated by the two forms of *Papilio turnus* which were long considered as distinct species until the rearing of their larvae proved them to be the same species.

A comparative study of larval and adult structures would doubtless add to our knowledge of the homologies of various organs and would portray more clearly the evolution of their form and structure. This is illustrated by the fact that in the most generalized larvae the epicranial suture is always present and well defined while in the more specialized forms it is much reduced or obsolete. This is because the epicranial suture is indicative of a primordea condition, namely the line of closure of the gastrula.

Scope of Thesis. - The work herein presented is but a brief survey of the general morphology of seven forms representative of six subfamilies of the Chrysomelidae. It has been impossible, therefore, to make the study a truly com-

parative one because of the lack of species which would be necessary to complete such a series. However, the object of the study has been more to survey the morphological characters with a view to determine their value in the formation of tables for the classification of the various larval species.

Acknowledgements. - The writer wishes to express his gratitude to Professor A. D. MacGillivray for his kind supervision of the study and also for the use of larvae which were in his collection.

II. THE MORPHOLOGY OF THE LARVAE

In general the morphology of the various types which have been selected is quite similar. With this in mind one type has been described in detail, and to avoid repetition only the variation from this type has been described in the remaining forms. The larva chosen for the type form is that of the Colorado potato-beetle, *Leptinotarsa decemlineata*. This species was taken because it seems to hold a central position so far as generalization and specialization are concerned. Further, the genus *Leptinotarsa* is one of a number of closely allied genera which constitute the major portion of the chrysomelid fauna of North America, so that the type is representative of the characters found in the most important and common genera.

III SUBFAMILY CHRYSOMELINAE

The beetles constituting the subfamily Chrysomelinae are most all oval, convex forms like the common Colorado potato-beetle. The larvae of Chrysomela and Leptinotarsa have large rounded abdomens, while those of the remaining genera are more flattened and resemble the larvae of the Galerucinae.

Leptinotarsa decemlineata

In form the larva of *Leptinotarsa* is grub-like (Fig.1). The Head is well chitinized and is globular in form and slightly smaller than the prothoracic segment. The prothoracic segment has a well defined dorsal shield. The mesothorax and metathorax are for the most part membranous and the latter segment is broadly joined to the abdomen. The legs are short and thick; their segments seem to be homologous with those of the adult. The abdomen is broad and strongly convex.

The Head

In describing the morphology of the head the subject has been divided into two divisions, namely, the fixed parts of the head, which deals with the sclerites of the head capsule and second, the movable parts of the head, which includes the antennae and mouth-parts. In all but one species described the mouth is directed ventrad in the natural position and all descriptions are made as if in this position.

The Fixed Parts.- The head capsule of *Leptinotarsa* (Figs. 16 and 17) is globular in form and slightly compressed.

The integument is strongly chitinized often to such an extent that the primary sutures are obliterated.

The epicranial suture appears as a distinct line on the dorso-meson. Starting at the large opening of the occipital foramen, it extends cephalo-ventrad to about the middle of the head where it bifurcates, sending its branches cephalo-laterad toward the antennal sockets. The stem of the inverted Y-shaped epicranial suture is wider than the arms and appears as a transparent suture. The distal ends of the arms of the suture become less clear and are obsolete about midway between the point of bifurcation and the antennal sockets.

The vertex consists of the area on the dorsal aspect of the head which is divided by the epicranial suture. It extends from near the occipital foramen cephalo-ventrad to the arms of the epicranial suture. Laterad on the dorsal half, the vertex extends almost to the occipital foramen where it fuses with the occiput, and on the ventral half it is bounded by the gena. The fusion of the vertex and the occiput is not marked by a suture.

The front is an unpaired subtriangular sclerite located cephalo-ventrad of the arms of the epicranial suture. The ventral boundary of this sclerite is not marked by a suture where it merges with the postclypeus, however, its limits are usually marked by a row of prominent setae or a sculptured surface. The lateral limits of the front are not definitely marked in this species because the ventral ends of the lateral arms of the epicranial suture are obsolete. A comparative study of

other forms of this family shows that the mesal margin of the antennal fossae probably marks the lateral boundary of the front.

The postclypeus is located ventrad of the front and is fused with its ventral margin. The line of fusion is usually indicated by a row of setae. The ventral margin of the postclypeus is marked by a distinct suture, the clypeal suture, and its lateral limits by the trochantins of the mandibles. Most morphologists consider this area as a part of the front.

The preclypeus is the broad quadrangular sclerite ventrad and adjacent to the postclypeus. It is commonly known as the clypeus. In most chrysomelid larvae it is a distinct sclerite and frequently it bears a transverse row of prominent setae.

The labrum is an unpaired semicircular sclerite borne on the ventral margin of the preclypeus. The median portion of the ventral margin is deeply emarginate. On either side of the emargination it is fringed with fine setae. The labrum is a movable flap surrounding the cephalic margin of the mouth opening and is analogous to the upper lip .

The occiput is the narrow sclerite located on the dorso-caudal aspect of the head and surrounding the dorsal half of the occipital foramen. The suture separating the occiput and vertex is obsolete.

The gena is the name sometimes applied to the lateral and caudal area of the head. It is not a sclerite but a part of the vertex. The mesal margins of the gena form the boundary of

the ventral half of the occipital foramen. The thickened ridge on each postgena is known as the crassa.

The corpotentorium is the narrow chitinized bar connecting the two postgenae. It is an internal structure of the head capsule.

The occipital foramen is the large elliptical opening on the caudal aspect of the head capsule. The dorsal half of the foramen is bounded by the occiput and the ventral half by the postgenae. The occipital foramen is the opening through which the alimentary canal and other organs pass into the thorax.

The trochantin of the mandible is the small crescent-shaped sclerite located ventrad of each antennal fossa. It is connected with the mandible by a tough membrane.

The ocelli or simple eyes are located on the vertex laterad of the ends of the epicranial suture. They are clear lenticular areas projecting above the surface of the vertex. In this genus there are six ocelli (Fig. 18). For reference they are numbered as follows: ocellus one is the most dorsal, ocellus two is ventro-cephalad of one, ocellus three is caudad of two or caudo-ventrad of one, ocellus four is ventrad of one or ventro-cephalad of three. These four ocelli form a quadrangle dorsad of the antennal fossa. The fifth ocellus is in line with two and four and is located some distance caudo-ventrad from them. Ocellus six is caudo-ventrad of ocellus five. In most forms ocelli five and six are caudad of the antennal fossae but their position is not as constant as that of the first four.

The size of the ocelli varies in the different species of the group. In *Leptinotarsa ocellus* five is the smallest.

The antennal fossae or openings in which the antennae are attached, are circular in outline, and are located ventrad of the quadrangular group of ocelli. In other members of this family they vary in position and are either distinctly located on the vertex or in the epicranial suture. Their location will be discussed more fully when the antennae are considered.

Movable Parts. - The antennae (Fig. 43) are located on the vertex ventrad of the quadrangular group of ocelli. They consist of three short segments, the proximal segment or scape has its attachment on a broad membranous area which is more or less convex. This segment is broader than long and is quite strongly chitimized. The second segment or pedicel differs from the first only in being smaller. The third segment is cone-shaped, with two or three terminal setae. Adjacent to the proximal end of the third segment is a conical digit about half as large as the third segment.

The apparent location of the antennae on the front seems to be due to the obliteration in part of the arms of the epicranial suture. The embryological development of insects indicates that the antennae are primarily located near the suture between the front and the vertex. This seems to be substantiated by the fact that in the more generalized larvae, namely *Phyllobrotica*, *Dibolia*, and *Chelymorpha*, the antennae are located in the slightly chitimized area which is a continuation of the

epicranial suture (Figs. 14, 20, 21, and 23).

The mandibles are the strongly chitinized wedge-shaped appendages attached to the ventro-lateral margins of the head capsule. The mesal margin of the mandible is sharply edged and the distal margin is five-dentate. For further reference the teeth are numbered in their order from one to five: number one being the most dorsal tooth (Figs. 23 and 24). The mandibles are hinged to the head capsule in part by a tough membrane attached to the ventral margin of the trochantins, on the cephalic margin by a small condyle which articulates in the postclypeal acetabulum and on the caudal margin by a strong condyle which fits into the postgenal acetabulum.

The maxillae (Fig. 31) are the less chitinized appendages located caudad of the mandibles. Normally in the adult beetle, the maxilla consists of a cardo, stipes, subgalea, palpifer, maxillary palpus, galea, and lacinia. In the larvae some of these structures are indistinguishable. The cardo is present and distinct. It is the proximal, rhomboidal sclerite, the dorsal angle or condyle of which articulates with the postgena. There is a prominent seta near its lateral margin. Attached to the cardo is the stipes. This is a large quadrangular sclerite. Its mesal margin is fused with the membrane bordering the labium, and the lateral margin with the cervical membrane. The subgalea is indistinguishable. The galea is represented by a small triangular sclerite at the ventro-mesal angle of the stipes. In the center of the galea is a prominent sensory pore and the mesal margin is bordered by a row of fine setae. The

palpifer is the narrow crescentic sclerite located in the membrane at the distal end of the stipes. It bears two large setae. The maxillary palpus is three-segmented. The two proximal segments are flattened, the first bears a single sensory pore and the second three setae. The third segment is conical and at the distal end are numerous short conical setae.

The labium (Fig. 31) is the unpaired appendage located between the maxillae. It is a large quadrangular piece with two short appendages at the distal end. The proximal part of the labium is a thinly chitinized area bearing on each side three large setae. It is composed of the fused submentum and mentum. The ligula is the small lobular piece forming the distal portion of the labium. The proximal part of the ligula is a narrow transverse band with a large seta on each side of the meson. At the distal end of the ligula there is a thin lobiform membrane representing the fused paraglossae. The labial palpi are the two segmented appendages laterad of the paraglossa. The first palpal segment is about as broad as long, the second is conical and bears at the distal end numerous subconical setae.

In life the head and mouth-parts are black or dark brown in color.

The Thorax

The thorax consists of three distinct segments, namely the prothorax, mesothorax and metathorax (Fig. 1). The prothorax has on its dorsal surface a distinct dorsal shield. In living specimens the cephalic half of the shield is orange-red in color, the remaining part is dull black. Ventrad of the lateral margins of the dorsal shield there are two black chitinized sclerites close to the first segment of the leg. The anterior of these sclerites articulates with the coxa and in all respects is doubtless homologous to the episternum of the adult. The caudal sclerite does not articulate with the coxa and it seems to be homologous with the epimeron of the adult. The remaining parts of the thorax are membranous.

The mesothorax is mostly membranous. The dorsal surface is marked by a deep fold dividing it into two annuletes, each of which is marked by two black spots. On the lateral aspect there is a black triangular spot which indicates the position on the ental surface the developing imaginal disc of an elytron. Cephalad of this, located in an oval spot, is the mesothoracic spiracle. The spiracle is a small, inconspicuous, circular opening in the center of the oval spot. This spiracle is located in the suture between the first and second thoracic segments. The episternum and epimeron of the mesothorax are slightly larger than those of the prothorax.

The metathoracic segment is large, membranous, and broadly joined to the abdomen. The dorsal surface is marked by

a shallow fold which divides it into two annulets. The lateral area bears a black triangular spot which is the position of the metathoracic imaginal disk. These thoracic spots which indicate the position of the developing wings, are present in most chrysomelid larvae. They have been termed the wing-spots by Tower. The episternum and epimeron are like those of the preceding segments.

The Thoracic Legs. - The thoracic legs of this larva are of moderate length, strongly chitinized, and adapted for clinging to stems and leaves of plants. The legs of each thoracic segment are so similar that it is only necessary to describe one of them. In this case the right mesothoracic leg is described and figured. (Fig. 52.).

The coxa is the proximal segment. It is cylindrical in form, strongly chitinized except for a small area on the dorsal third toward the distal end. It is joined to the body by a tough membrane and articulates against the coxal process of the episternum. The trochanter and femur are fused and appear as a single segment, however, there is a suture which marks the limit of the former segment. This suture is clearly defined on the dorsal and lateral surfaces, it arises near the point of attachment with the coxa and extends latero-ventrad forming a small triangular segment. The femur is cylindrical and slightly smaller toward the distal end. The tibia is the longest segment of the leg, it is cylindrical in form, and is slightly chitinized on the ventral aspect. The tarsus is represented by a single sharply hooked claw-like segment.

The Abdomen

The abdomen (Fig. 1) is broad, strongly convex, and composed of ten membranous segments. Segments one to seven are similar in form and marking. On the lateral area of each segment there are two black pigmented areas. The dorsal one of these, on segments one to eight, contains in the center a circular spiracle. The spots, which bear the spiracle, may be known as the spiracular spots. Ventrad of each spiracular spot is an oval black area which has been called the baso-pleural spot. The eighth segment differs from the seventh in having a broad black tergal area and a smaller spiracular spot. The ninth and tenth segments are fused and appear as a single segment. This segment functions as an anal proleg.

The abdominal spiracles occur on segments one to eight inclusive. They are circular in outline with a slightly raised margin.

In life the abdomen of the larva is a bright orange-red color with all maculations black.

IV SUBFAMILY GALERUNCINAE

The members of the subfamily Galerucinae are among the most serious of agricultural pests. The well-known striped cucumber beetle, the long-horned corn beetle and the elm-leaf beetle are representatives of the subfamily. Since the larvae may be leaf-feeders or root-feeders, two examples of the group are figured and described.

Galeruca sp.

The larvae of *Galeruca* are elongate and cylindrical in form resembling certain Lepidopterous larvae. (Figs. 12,13). The head is of moderate size and black in color. The thorax and abdominal segments are similar in size and general arrangement of papillae and setae. The body color is a pinkish brown, the papillae are gray, each terminating with a single black seta. The legs are black. The species here described is common on willow.

The Head

Fixed Parts.- The epicranial suture differs from that of *Leptinotarsa* in that its arms terminate at the dorsal margins of the antennal fossae, thus defining the frontal area. (Fig. 19).

The ocelli are reduced in number to a single ocellus on each side of the head. They are located on the vertex dorsad of the antennal fossae and from their position would seem to be homologous to ocelli two of *Leptinotarsa*.

The remaining fixed parts of the head capsule do not differ decidedly from those of the preceding species.

The Movable Parts. - The antennae (Fig. 44) consist of

two segments, the proximal one is more or less retracted into the cushion-like antennal membrane. The second or distal segment is conical in form and is considerably smaller than the first. Adjacent to the base of the second segment there are three minute conical setae (Fig. 44).

The mandibles of *Galeruca* differ from those of the preceding species in having only four teeth, the fifth is obsolete (Fig. 25)

The maxillae (Fig. 32) of this species is different from that of *Leptinotarsa*. The cardo is small and triangular, the stipes, palpifer and maxillary palpus show no marked changes. The galea consists of a knob-like appendage bearing two small digit or projections and several setae. In addition to the parts already noted is a well-defined lacinia. It is a comb-like organ located on the cephalo-mesal area of the maxilla (Fig. 33).

The labium (Fig 32) in this species is membranous. The labial palpi consist of two segments.

The Thorax

The dorsal and lateral areas of the thorax are armed with a number of papilliform protruberances, each of which terminates in an erect black seta (Fig. 12). On the prothorax the cephalic margin is fringed with eighteen papillae. The segment caudad of the marginal fringe has a median transverse row of six papillae. On the mesothoracic and metathoracic segments the protruberances are similarly arranged, however, in the median transverse row there are only four papillae, and on the lateral area the papillae are arranged in groups of three. The meso-

thoracic spiracles occupy a position between the first and second thoracic segments. The sternal area has but a single papilla laterad of each coxal segment. (Fig. 13)

The episternum is present in the form of a slightly chitinized triangular sclerite located cephalad of each coxal segment and articulating with its coxal process. The epimeron is obsolete.

The Thoracic Legs. - The legs of this larva are formed for walking and clinging to leaf surfaces. The segmentation is like that of *Leptinotarsa*, however, in this species the tarsus is fused with the claw and membranous pulvillus (Fig. 53).

The Abdomen

The abdomen consists of nine distinct segments, similar in form and size to those of the thorax. Segments one to seven have a similar setal arrangement, which differs from that of the thorax in that only two papillae constitute the transverse row of each segment. The lateral papillae are three in number arranged one above the other, forming an oblique row. (Fig. 12.) The spiracles of these segments are located cephalad of the second lateral protruberances. The papillae of the eighth segment are arranged like those of the preceding segments but are inclined caudad instead of being erect. The spiracle holds the same position as described for the other abdominal segments. The ninth and tenth segments are fused and appear as a single segment. This segment functions as a single disc-like anal proleg.

The abdominal spiracles are eight in number. They

are black circular openings somewhat raised above the surrounding surface. The eighth spiracle is notably smaller than those on the other segments.

Phyllobrotica descoidea

In the genus *Phyllobrotica* the larvae live in the soil and feed upon the roots of various plants. They are elongate, cylindrical, white grubs with small black heads and thoracic legs. Figure 4 is that of *Phyllobrotica descoidea*, one of the root-feeding species of the *Galerucinae*.

The Head

Fixed Parts. - The head capsule of this larva presents several interesting modifications which are not present in either of the preceding species (Fig. 20).

The epicranial suture is a broad membranous area in the form of an inverted V, the stem of the suture being lost. The arms of the suture extend ventro-laterad to the antennal fossae enclosing them in a slightly chitinized area.

The vertex has the same extent as described for the preceding forms, however, the first trace of its modification is shown by the deep emargination on the caudal margin, in the region of the occiput (Fig. 20).

The preclypeus shows a tendency to become fused with the postclypeus by the obliteration of the suture which separates these parts.

The labrum in this larva is much broadened. Its cephalic area and ventral margin bears a number of prominent blunt setae (Fig. 20).

The ocelli are obsolete.

Movable Parts. - The antennae consist of two segments which are short and cylindrical in form. The distal end of the first segment is encircled by short conical setae (Figs 45 and 46).

The mandibles are strong wedge-shaped appendages, entirely without teeth but with the mesal and distal margins formed into a sharp cutting edge (Fig. 26).

The maxillae and labium are broadly fused (Fig. 34). The cardo is not a distinct segment but consists of a strongly chitinized piece which is fused with the membrane of the stipes. The lacinia is wanting.

The Thorax

The thorax is largely membranous. The prothorax has a small chitinized dorsal shield and the mesothorax and metathorax bear a number of slightly chitinized centers scattered over the dorsal and lateral areas (Fig. 4). The wing-spots of the second and third thoracic segments are prominent. The mesothoracic spiracle is located cephalad of the mesothoracic wing-spot near the suture between the first and second thoracic segments.

The Thoracic Legs. - The legs of this larva are similar in form and segmentation to those of *Galeruca* (Figs 54 and 55.)

The Abdomen

The abdomen is long and cylindrical and is composed of ten distinct segments. Segments one to eight are composed

largely of delicate white membrane, which under high magnification has a peculiar reticulate marking (Fig. 63). There are also a number of slightly chitinized areas on the dorsal and lateral areas of these segments. The ninth and tenth segments are fused but the latter segment may be identified as a small finger-like projection or anal proleg. The dorsal aspect of the ninth segment is flattened and chitinized, forming a well defined suranal plate.

The abdominal spiracles are eight in number and appear as minute circular spots on the lateral aspect of segments one to eight.

V SUBFAMILY HALTICINAE

The members of this subfamily constitute the large group of jumping chrysomelids commonly known as "flea beetles" or "jumping beetles." The larvae are mostly leaf-feeders and resemble very closely the larvae of the Galerucinae. A few, however, are leaf-miners.

Dibolia borealis

The larvae of *Dibolia borealis* (Fig. 5) is a leaf-miner in the leaves of plantain. The form and structure of the larvae has been modified by this mode of life. The body is long, fusiform, depressed, and entirely without chitinous areas. The head is small and the mouth is directed cephalad. The legs are much reduced in length.

The Head

Fixed Parts. - The epicranial suture (Figs. 21 and 22) consists of two branches or arms, the stem of the suture is obsolete. The arms extend from the occipital foramen cephalo-laterad to the caudal margins of the antennal fossae.

The vertex is deeply cleft by a V-shaped emargination which divides it into two lobes which are retracted into the prothoracic segment.

The front is the broad triangular area cephalad of the arms of the epicranial suture. It is united with the post-dypeus on the cephalic boundary.

The preclypeus is not separated from the postclypeus by a distinct suture, but in cleared specimens a faint clypeal suture may be traced.

The labrum is small and lobiform, its cephalic margin is fringed with numerous flattened setae (Fig. 21). The occipital foramen is very large in heads of this type, due to the caudal extension of the lobes of the vertex. (Fig. 22)

The ocelli are wanting.

The Movable Parts. - The antennae (Figs. 48 and 49) are located on the sides of the head at the cephalic ends of the arms of the epicranial suture. The scape is cylindrical in form and on the cephalic and caudal aspects are three sensory pores which appear as clear circular spots. At the distal end of the scape there are five large setae and a small second antennal segment.

The mandible is deeply concave on its mesal surface and at the distal margin are four large teeth. The postgenal condyle is large (Fig. 27).

In the maxilla the cardo is fused with the stipes, and the palpifer and galea are fused forming a separate sclerite which is separated from the stipes by a transverse suture (Fig. 36). The maxillary palpi have three segments.

The labium is partly chitinized on the proximal half. The ligula is membranous and closely set with rows of minute sharp setae (Fig. 37). The labial palpi are obsolete.

The Thorax

The thorax is entirely membranous with the exception

of the slightly chitinized, crescentic wing-spots of the mesothorax and metathorax. The thoracic and abdominal membrane, when highly magnified, appears to be covered with minute irregular granules (Fig. 62) . The mesothoracic spiracle is located cephalad of the mesothoracic wing-spot in the suture between the first and second thoracic segments.

The Thoracic Legs. - The legs are reduced in length, but the segmentation is similar to that of the preceding species. The coxa is broadly joined with the body, the trochanter and femur are fused and the tarsus consists of single claw-like segment with a pulvillus (Figs. 56, 57, and 58).

The Abdomen

The abdomen is elongate, depressed, and tapers toward the caudal end. It is composed of nine membranous segments which are entirely without setae and chitinous areas. On the lateral aspect of each segment, except the ninth, the body-wall is projected into a wart-like protruberance. The abdominal spiracles are located cephalad of these protruberances and occur on segments one to eight inclusive. The ninth and tenth segments are fused.

VI SUBFAMILY CASSIDINAE

The subfamily Cassidinae includes a comparatively small group of oval, convex beetles having the elytra and pronotum expanded beyond the body outline and suggesting the form of the carapace of a tortoise. From this superficial resemblance the popular name "tortoise-beetles" has been derived.

The larvae are oval, flattened grubs with long lateral spines. At the caudal end of the body is a forked process which is bent cephalad over the back and on which the larvae carry their cast-off skins and excrement, forming a shield-like covering or parasol, which is supposed to protect the larvae from their enemies.

Chelymorpha argus

The larva of *Chelymorpha argus* (Fig. 2) is oval and flattened in form. The lateral margin of the body armed with thorny spines, and at the caudal end of the body there is a long bifurcate spine or faeci-fork. The body color is a greenish yellow with all maculations and processes in black.

The Head

Fixed Parts. - The epicranial suture bifurcates shortly cephalad of the occipital foramen (Fig. 14). The arms of the suture curve cephalo-laterad toward the ocelli where they broaden out into a slightly chitinated area mesad of ocellus two. From the ventral angle of this broadened area a narrow suture extends ventrad to each antennal fossa, and surrounds it by a thinly

chitinized membrane.

The vertex has the same form and extent as described for that of *Leptinotarsa*.

The front in this insect has been modified in outline through the bending of the arms of the epicranial suture.

The preclypeus and labrum are well defined and in shape are like those of *Leptinotarsa*.

The trochantins of the mandibles are well developed and appear as distinct sclerites at the proximal end of the mandibles.

The ocelli are six in number. They are located on small wart-like projections dorsad of the antennal fossae (Fig. 15). The arrangement of the ocelli is similar to that of *Leptinotarsa*.

Movable Parts. - The antennae consist of three segments. The scape and pedicel are short and cylindrical in form and at the distal end of the latter are four conical setae and a small pointed third segment (Fig. 47).

The mandibles are strongly chitinized and have four tooth-like projections on their distal margin (Fig. 28).

The maxilla (Fig. 35) has been modified by the fusion and reduction of parts. The cardo is fused with the stipes so that it is indistinguishable as a separate sclerite. The galea and palpifer are also fused and appear as a single sclerite at the end of the stipes. The maxillary palpus has but two segments.

In the labium (Fig. 35) the submentum and mentum are membranous and are fused as in all the forms which have been

described. The ligula is strongly chitinized except for a small membranous area near the proximal end of the labial palpus, which consists of a single segment.

The Thorax

The thoracic segments are broad and flattened (Fig. 2). The dorsal aspect of the prothoracic segment has a broad dorsal shield and the lateral margins are armed with six thorny spines (Fig. 3). The mesothoracic segment is membranous and bears four lateral spines. The spiracle of this segment is located on the side in the suture which separates the first and second thoracic segments. The metathorax is similar in structure to the preceding segment, but has two lateral spines.

The Thoracic Legs. - The legs (Fig. 59) of this larva are reduced in length by the fusion and shortening of the segments. The coxa is represented by a small crescentic sclerite attached closely to the membrane of the thorax. The trochanter and femur are fused forming only a short segment. The tibia is thick and finger-like in form and has the distal end modified into a pulvillus-like cushion. The tarsus is fused and is represented by a single claw-like structure which is deeply inserted in the distal end of the tibia.

The Abdomen

The abdomen is oval in outline and much depressed. It consists of ten membranous segments, seven of which are short and very broad. The lateral margin of each segment is armed

with a single thorny spine. The spiracles of these segments are located on the dorsal aspect mesad of the proximal end of each spine or process. The eighth segment is lobiform and has near its cephalo-mesal margin a spine and spiracle similar to the preceding segments, while the caudal margin is produced into a bifurcate process or faeci-fork (Fig. 2). The ninth and tenth segments are fused to form a single anal proleg.

VII SUBFAMILY CHLAMYDINAE

The larvae of this subfamily have the curious habit of enclosing themselves in tight cases which are composed of their own excrement. They carry these cases about with them much like the case-bearing larvae of certain moths. When ready to pupate the case is fastened to a twig and the opening is closed, thus making them answer the purpose of a cocoon.

Chlamys plicata

The larva of *Chlamys plicata* illustrate certain modifications of body form due to the case-dwelling habit. The resulting changes are manifest in the lengthening of the thoracic legs and the sack-like form of the abdomen. (Fig. 8).

The Head

Fixed Parts. - The epecranial suture (Fig. 9) has a long narrow stem extending from the occipital foramen to about the center of the cephalic aspect of the head, where it bifurcates. The lateral arms of this suture extending latero-ventrad almost to the antennal fossae where they bend laterad around them and end at the suture dorsad of the trochantius of the mandibles.

The vertex shows no decided modifications from that of *Leptinotarsa*.

The front is the triangular sclerite ventrad of the

arms of the epicranial suture, its ventral margin is fused with the postclypeus.

The clypeal suture in this species is almost obsolete and can only be traced in cleared specimens (Fig. 9).

The labrum (Figs. 9 and 10) is the lip-like sclerite attached to the ventral margin of the preclypeus. The ventral margin of this sclerite has four groups, each composed of three flattened setae.

The trochanitins of the mandibles are represented by a crescentic membranous area at the proximal ends of the mandibles.

The ocelli are six in number and they are grouped like those of the type form (Figs. 11 and 18). Ocelli one and three are larger than two and four and ocellus five is the largest of the entire group.

Movable Parts. - The antennae (Fig. 50) are composed of three segments, the two basal segments are flattened and cylindrical, the third is a small conical digit at the distal end of the second segment.

The maxillae are similar in structure to the type form. The cardo is a distinct triangular-shaped sclerite. The stipes is the large, quadrangular sclerite which bears at the distal end the galea and maxillary palpus. The galea is peculiar in that the caudal aspect is composed of a delicate membrane, the mesal margin of which is fringed with a row of broadly flattened setae; its cephalic aspect is smooth and chitinous (Figs. 38

and 39). The palpifer is a distinct segment at the base of the maxillary palpus, but it is distinguished from the latter by the two prominent setae which are common to this sclerite.

The labium (Fig. 38) differs from that of any of the other species in having the ligula separated from the mentum by a narrow membranous band. The glossae are only slightly membranous. The labial palpus consists of two segments.

The Thorax

During the entire larval life the only exposed parts of the body are the head, the prothorax, and thoracic legs. The modification of structure brought about by the sack-bearing habit seems to have had more effect on the thoracic parts than any other structures of the body. This is noted particularly in the prothorax (Fig. 8) which is protected by a broad dorsal shield covering the entire dorsal aspect. The proepisternum is strongly chitinized, particularly at the point of articulation with the procoxa. The proepimeron is large and chitinized. The surface of the mesothoracic segment is not exposed during the larval life, consequently the parts which do not have special muscular attachments are composed of delicate membrane. The mesothoracic wing-spot is a slightly chitinized oval area on the lateral aspect. The mesoperitreme is a small circular sclerite cephalad of the mesothoracic wing-spot. The mesospiracle is the small opening in the center of the mesoperitreme. The mesoepisternum and mesoepimeron are larger and more heavily chitinized than the proepisternum and proepimeron. The metathorax

is similar to the preceding thoracic segment except that it lacks a peritreme and spiracle.

The unusual development of the episternum and epimeron of each thoracic segment in this species is due to the fact that either the muscles are greatly enlarged or that extra muscles are attached upon these areas, which is necessitated by the increased weight of the body, and the case covering it.

The Thoracic Legs. - The thoracic legs are unusually long and very strongly chitinized. The coxa is long and cylindrical in form and in this group reaches its maximum development. The trochanter is short and fused with the femur, although the line of fusion is marked by a suture. The femure is much lengthened. The tibia is about as long as the combined trochanter and femur. The tarsus consists of a single claw-like segment (Fig. 60).

The Abdomen

In life the abdomen is entirely enclosed in a protecting case, consequently the form has been modified under these conditions into a delicate membranous sack, with the caudal end bent ventro-cephalad, placing the anal opening near the mouth of the enclosing case (Fig. 8). The abdomen consists of ten segments. The dorsal aspect of the first four are crossed by numerous folds which make the segmentation indistinct. Segments four to six are very large and much longer and wider on the dorsal aspect, segments seven to ten successively are smaller, and segment ten tapers to a rounded point which is directed cephalad. The ninth and tenth segments are distinct. The abdominal spiracles are

located on small elliptical spots on the lateral aspects of segments one to eight.

VIII SUBFAMILY DONACIINAE

The beetles constituting the subfamily Donaciinae are among the most beautiful of this family. They are elongate in form and resemble very closely certain species of Cerambycidae. For this reason systematists have placed this subfamily next in the list, thus indicating that they are a connecting link with the Cerambyciⁱdae. Contrary to this view the Donaciinae are placed last in this paper, which indicates that they are considered as the most specialized members of the family Chrysomelidae. This conclusion is based on a study of the larvae, but it is believed that a careful study of the morphology of the adults would lead to the same conclusion.

Donacia sp.

The larvae of Donacia (Fig. 6) live on the roots and rhizomes of aquatic plants. They obtain their air supply by tapping the air-chambers in the rhizomes of aquatic plants. When about ready to pupate they enclose themselves in silken cocoons which are attached to the submerged rhizomes.

The Head

The head capsule of Donacia (Fig. 42) is elongate in outline and on the dorsal aspect is deeply emarginate. The epecranial suture is distinct and in the form of an ⁿinverted Y. The lateral arms of the suture become obsolete about half way between the point of bifurcation and the antennal fossa.

The vertex is bilobate on the dorsal aspect. Its

ventral and lateral boundaries are similar to those described for the type form.

The front is subtriangular in form and is outlined on its caudal margin by the epicranial suture; the ventral margin is fused with the postclypeus.

The preclypeus is a distinct quadrangular sclerite ventrad of the fused front and postclypeus (Fig. 42).

The labrum is the small, angular sclerite hinged to the ventral margin of the preclypeus. The cephalic aspect is armed with eight setae and the ventral margin with four groups each, composed of two setae.

The ocelli are wanting in the species studied although in some members of this genus there are as many as five ocelli.

Movable Parts. - The antennae (Fig. 51) are composed of three segments. The scape is short and cylindrical and on the cephalic aspect there are three large sensoria. The pedicel is slightly smaller than the scape and at its distal end is the conical third segment and a small accessory digit.

The mandibles (Fig. 30) are small triangular-shaped appendages with two rounded teeth near the distal end of the ventro-mesal margin. The postgenal condyle is prominent.

The maxillae of *Donacia* are considerably different from the type form (Fig. 40). The cardo is the long triangular sclerite attached to the postgena on its mesal margin. There is ventrad of the cardo a short segment, the stipes, which bears two long setae on the lateral aspect. The ventral boundary of the stipes is indicated by a short suture which does not reach its mesal

margin. The palpifer is adjacent to this segment. This sclerite may be identified by the two lateral setae which are very close to one another and by the clear circular spot on the caudal aspect. A three-segmented maxillary palpus is attached to the ventral margin of the palpifer. The proximal segment is elongate and flattened on the mesal aspect and on the caudal aspect it bears two clear circular spots. The second segment is shorter than the first, its proximal half on the mesal aspect is flattened and near its distal margin are two small setae. The third segment is conical in form and has a number of short setae at the distal end. The galea is the strongly chitinized racket-shaped sclerite attached to the mesal margin of the fused stipes and palpifer.

The labium (Fig. 41) is a small membranous lobiform appendage located between the maxillae and in this larvae it is not fused with the maxillae as in all the preceding species. The ligula is separated from the mentum by a narrow chitinized band and its caudal aspect bears four setae. The labial palpus consists of a single segment with a sensory pore on the caudal surface.

The Thorax

The thorax (Fig. 6) consists of three rounded membranous segments with small setal patches on the dorsal and lateral areas. The prothorax is somewhat longer and more tapering than the mesothorax. The dorsal aspect of the mesothorax has two narrow transverse furrows which form three annulets. On the lateral aspect there is a small non-functional spiracle. The metathorax

is similar to the preceding segment except for the lack of spiracles. The episternum and epimeron are not chitinous.

The Thoracic Legs. - The thoracic legs of this larva are reduced to simple hooked appendages (Fig. 61). The coxa is represented by an enclosed elliptical membranous area on the body. The trochanter and femur are entirely fused. The tibia is a short conical segment and the tarsus is represented by a single curved claw-like segment.

The Abdomen

The abdomen consists of ten rounded membranous segments (Fig. 6). The caudal end of the body is bluntly pointed and is bent ventro-cephalad. The setae are distributed in irregular patches over the body surface. The arrangement of their setal areas has been used by MacGillivray as a means of determining the species of this genus. The segments one to seven are distinct and easily identified by their spiracles. The eighth segment (Fig. 7) is bent ventro-cephalad. It bears two long caudal spines at the base of which are two large spiracles, each surrounded by a chitinous plate or peritreme. There are cephalad of the peritremes two small chitinous areas which indicate the location of the dorsal apodeme or invagination of the body-wall, and cephalo-lateral of each peritreme are the large anterior sclerites. The ninth and tenth segments are not easily determined, the primary sutures are obsolete, however, by a careful study of their setal arrangement and folds MacGillivray concludes that

there are ten abdominal segments (Figs. 6 and 7).

There are nine pairs of spiracles present in this larva as in all the members of the family, however, the eighth abdominal spiracles are probably the only functional ones. The method of respiration in this subfamily is different from that of most aquatic larvae which breath by means of tracheal gills or blood gills. In *Donacia* the larvae puncture the air-chambers in the rhizomes of aquatic plants. This is accomplished by piercing the rhizomes with the caudal spines. As the air escapes from the puncture the large spiracles at the base of the spines are pressed close to the rupture where they collect the escaping air bubbles.

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X. LIST OF ABBREVIATIONS

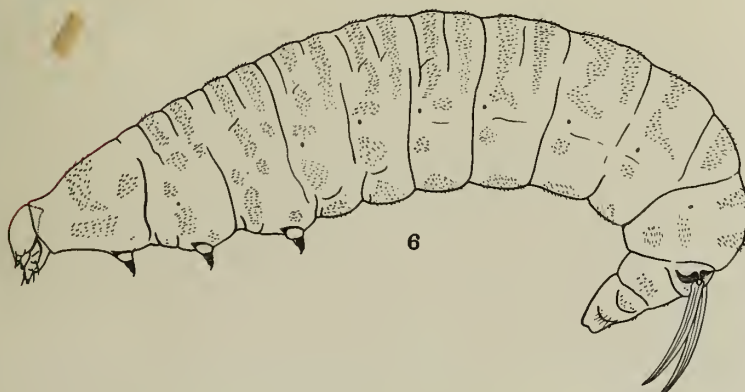
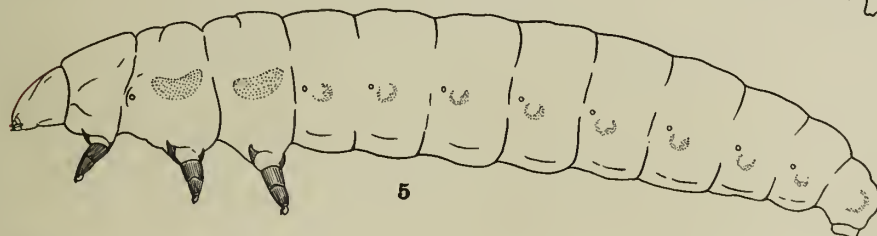
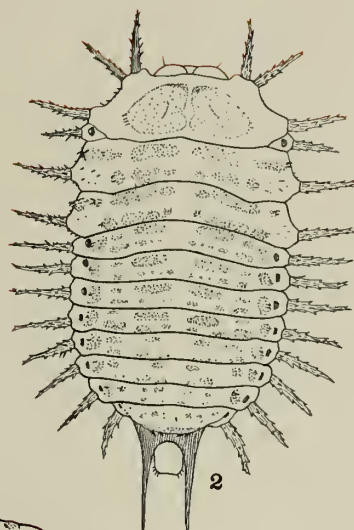
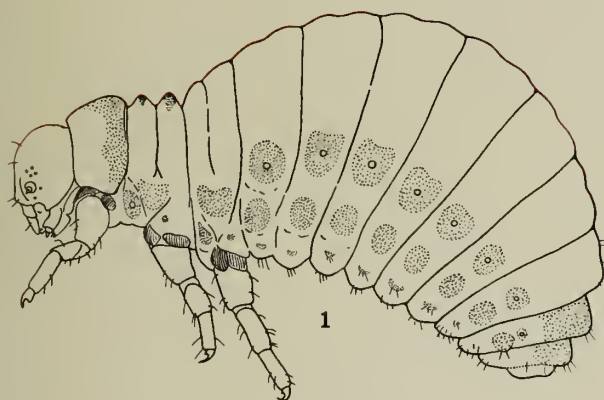
c.	. coxa
ca.	. cardo
ct.	. corpotentorium
e. s.	. epicranial suture
fe	. femur
fr.	. front
ga.	. galea
ge.	. gena
l.	. labium
la.	. lacinia
lg.	. ligula
l. p.	. labial palpus
lr.	. labrum
m.	. mentum
md.	. mandible
m.p.	. maxillary palpus
oc.	. ocelli
occ.	. occiput
pa.	. palpifer
pd.	. pedicel
poc.	. postclypeus
prc.	. preclypeus
sc.	. scape

em	submentum
st.	.stipes
ta.	.tarsus
ti.	tibia
tr.	.trochanter
tr.m.	.trochantin of mandible
v.	vertex

Explanation of Plate I.

- Fig. 1. *Leptinotarsa decemlineata*, lateral aspect.
Fig. 2. *Chelymorpha argus*, dorsal aspect.
Fig. 3. *Chelymorpha argus*, lateral spine.
Fig. 4. *Phyllobrotica discoidea*, lateral aspect.
Fig. 5. *Dibolia borealis*, lateral aspect.
Fig. 6. *Donacia* sp., lateral aspect.
Fig. 7. *Donacia*, dorsal aspect of caudal segments
 and spines.

Plate I.

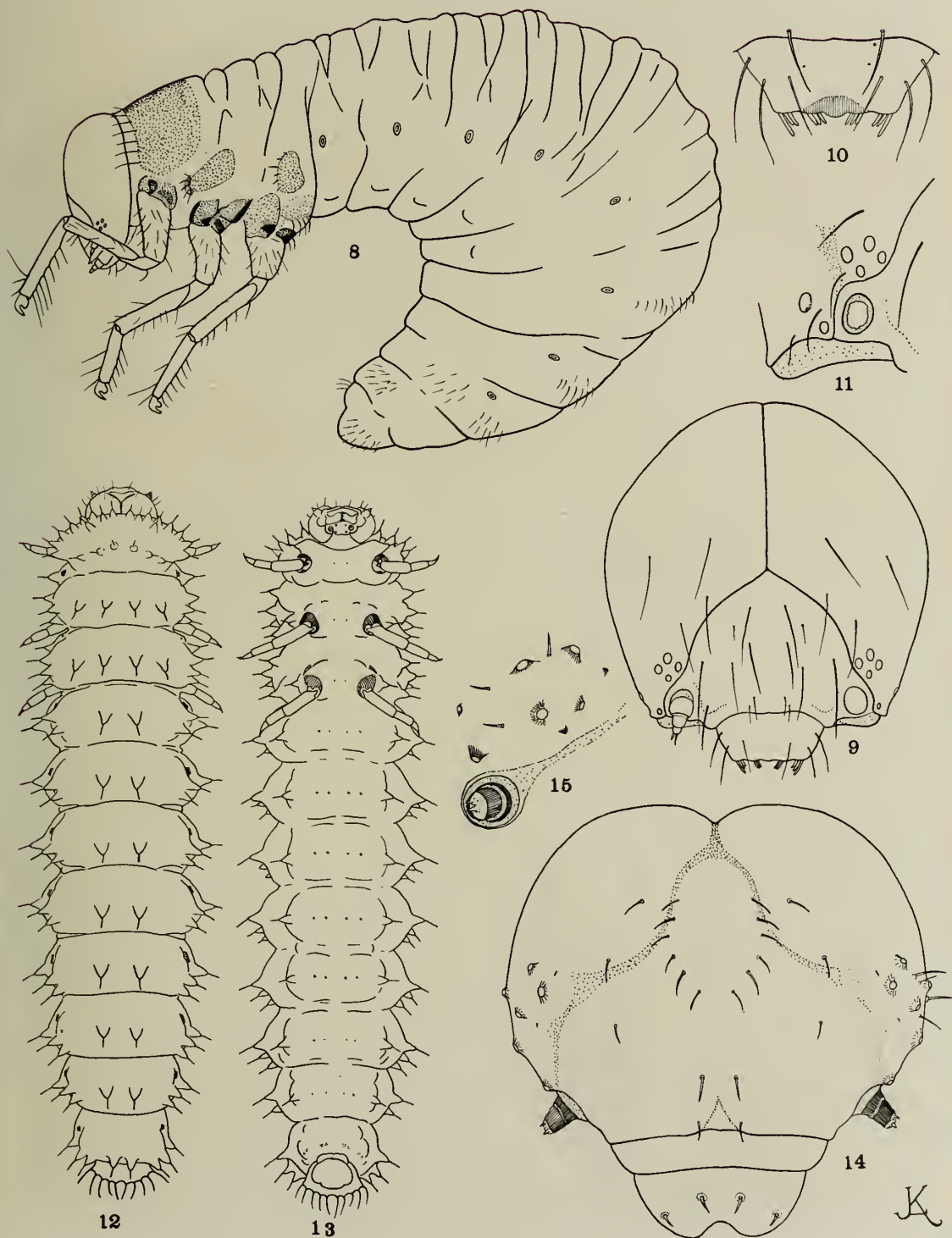


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Explanation of Plate II.

- Fig. 8. *Chlamys plicata*, lateral aspect.
- Fig. 9 . *Chlamys plicata*, cephalic aspect of head.
- Fig. 10. *Chlamys plicata*, cephalic aspect of labrum.
- Fig. 11. *Chlamys plicata*, detail of ocellar group.
- Fig. 12. *Galeruca* sp., dorsal aspect.
- Fig. 13. *Galeruca* sp., ventral aspect.
- Fig. 14. *Chelymorpha argus*, cephalic aspect of head.
- Fig. 15. *Chelymorpha argus*, detail of ocellar group.

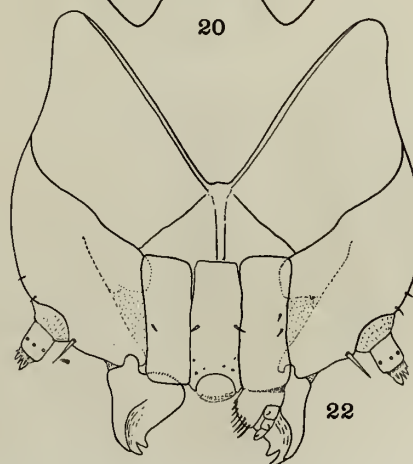
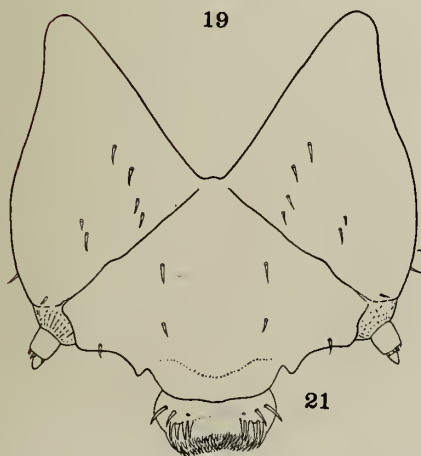
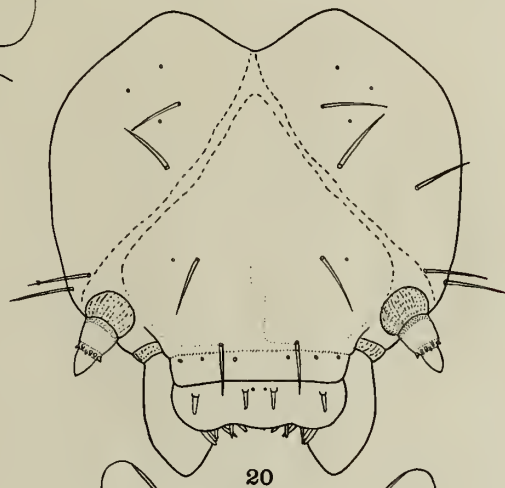
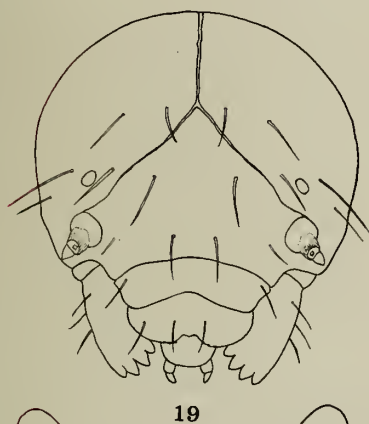
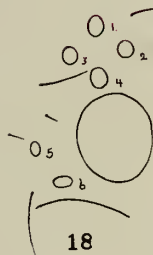
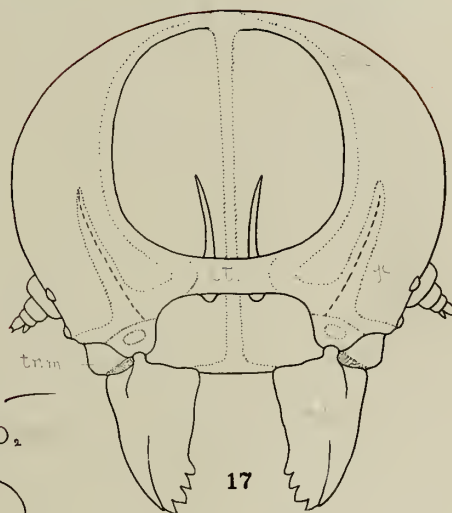
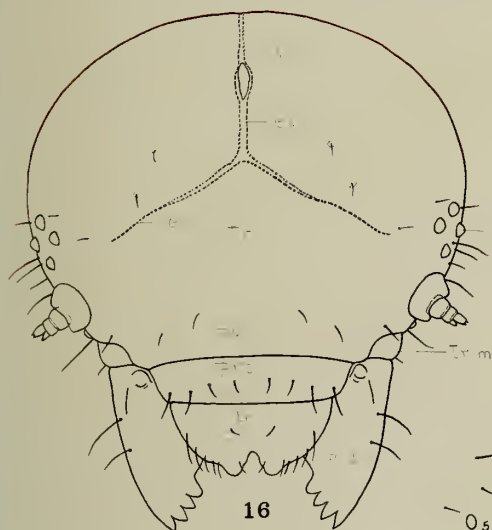
Plate II



Explanation of Plate III.

- Fig. 16. Leptinotarsa decemlineata, cephalic aspect
 of head.
- Fig. 17. Leptinotarsa decemlineata, caudal aspect
 of head.
- Fig. 18. Leptinotarsa decemlineata, detail of ocellar
 group.
- Fig. 19. Galeruca sp., cephalic aspect of head.
- Fig. 20. Phyllobrotica discoidea, cephalic aspect
 of head.
- Fig. 21. Dibolia borealis, cephalic aspect of head.
- Fig. 22. Dibolia borealis, caudal aspect of head.

Plate III.

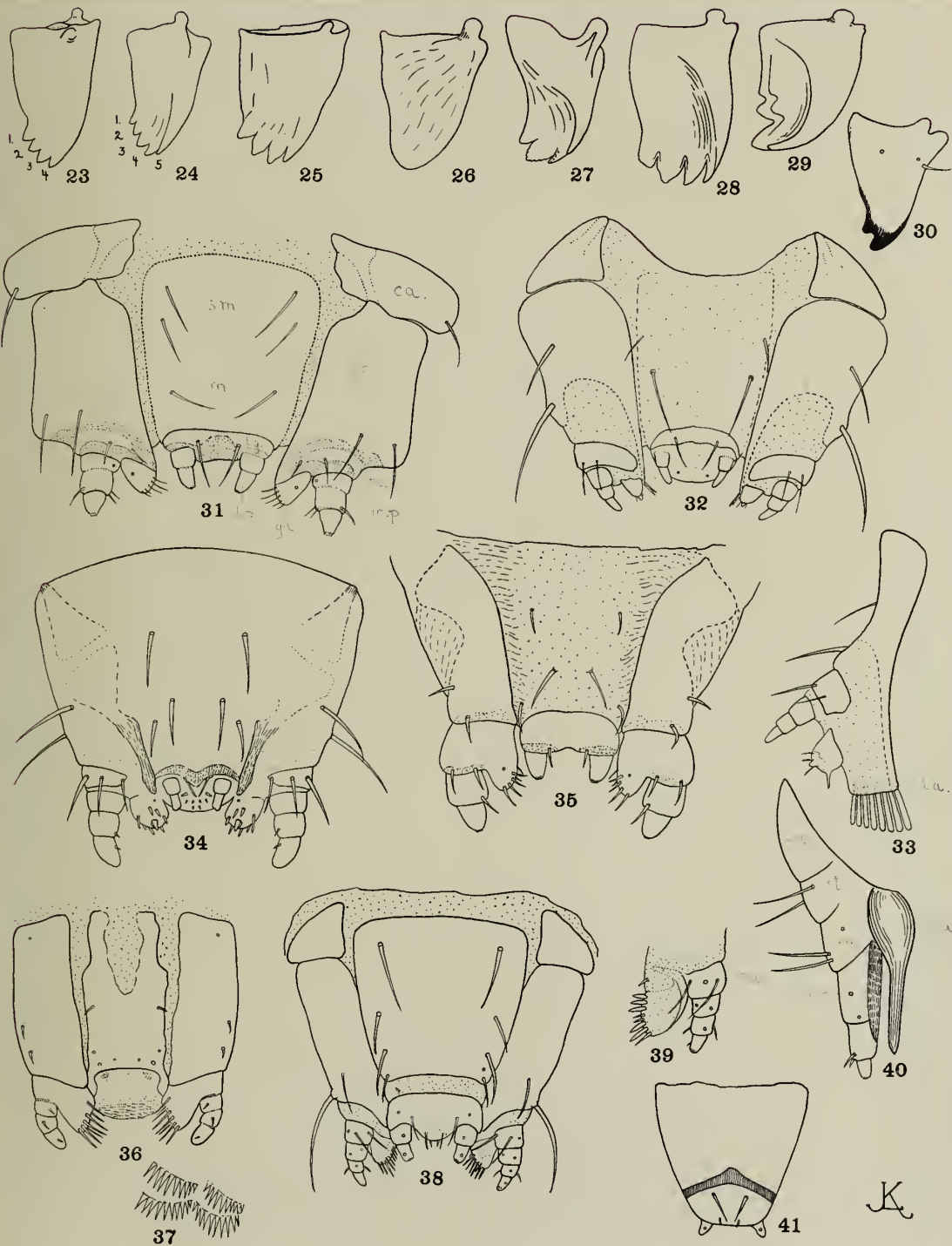


K

Explanation of Plate IV.

- Fig. 23. *Leptinotarsa decemlineata*, cephalic aspect of left mandible.
- Fig. 24. *Leptinotarsa decemlineata*, caudal aspect of right mandible.
- Fig. 25. *Galeruca* sp. caudal aspect of right mandible.
- Fig. 26. *Phyllobrotica discoidea*, caudal aspect of right mandible.
- Fig. 27. *Dibolia borealis*, caudal aspect of right mandible.
- Fig. 28. *Chelymorpha argus*, caudal aspect of right mandible.
- Fig. 29. *Chlamys plicata*, caudal aspect of right mandible.
- Fig. 30. *Donacia* sp., cephalic aspect of left mandible.
- Fig. 31. *Leptinotarsa decemlineata*, caudal aspect of maxillae and labium.
- Fig. 32. *Galeruca* sp., caudal aspect of maxillae and labium.
- Fig. 33. *Galeruca* sp., caudo-mesal aspect of maxilla.
- Fig. 34. *Phyllobrotica discoidea*, caudal aspect of maxillae and labium.
- Fig. 35. *Chelymorpha argus*, caudal aspect of maxillae and labium.
- Fig. 36. *Dibolia borealis*, caudal aspect of maxillae and labium.
- Fig. 37. *Dibolia borealis*, detail of setae from the ligula.
- Fig. 38. *Chlamys plicata*, caudal aspect of maxillae and labium.
- Fig. 39. *Chlamys plicata*, caudal aspect of galea and maxillary palpus.
- Fig. 40. *Donacia* sp., cephalic aspect of right maxilla.
- Fig. 41. *Donacia* sp., caudal aspect of labium.

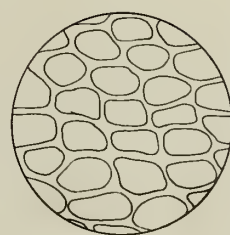
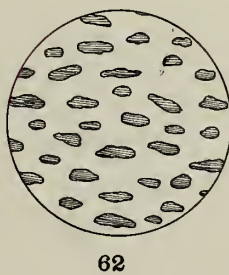
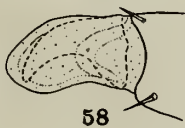
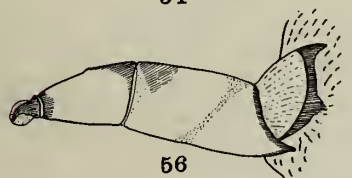
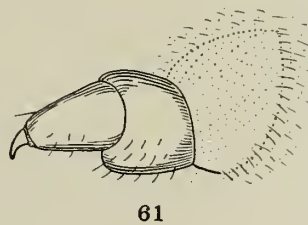
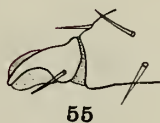
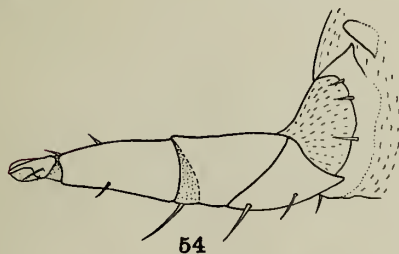
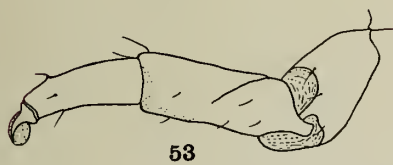
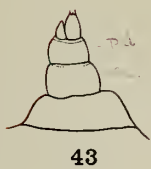
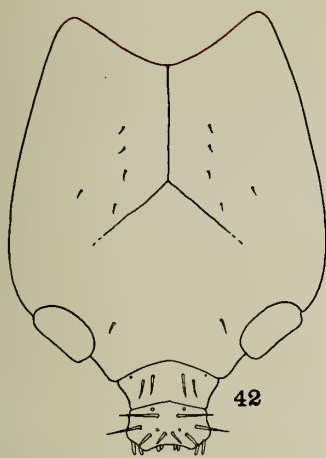
Plate IV.



Explanation of Plate V.

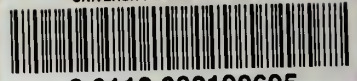
- Fig. 42. *Donacia* sp., cephalic aspect of head.
- Fig. 43. *Leptinotarsa decemlineata*, lateral aspect of antenna.
- Fig. 44. *Galeruca* sp., lateral aspect of antenna.
- Fig. 45. *Phyllobritica discoidea*, lateral aspect of antenna.
- Fig. 46. *Phyllobrotica discoidea*, distal end of antenna.
- Fig. 47. *Chelymorpha argus*, lateral aspect of antenna.
- Fig. 48. *Dibolia borealis*, cephalic aspect of antenna.
- Fig. 49. *Dibolia borealis*, caudal aspect of antenna.
- Fig. 50. *Chlamys plicata*, lateral aspect of antenna.
- Fig. 51. *Donacia* sp., lateral aspect of antenna.
- Fig. 52. *Leptinotarsa decemlineata*, cephalic aspect of mesothoracic leg.
- Fig. 53. *Galeruca* sp., cephalic aspect of mesothoracic leg.
- Fig. 54. *Phyllobrotica discoidea*, cephalic aspect of mesothoracic leg.
- Fig. 55. *Phyllobrotica discoidea*, cephalic aspect of tarsus.
- Fig. 56. *Dibolia borealis*, cephalic aspect of mesothoracic leg.
- Fig. 57. *Dibolia borealis*, cephalic aspect of tarsus.
- Fig. 58. *Dibolia borealis*, caudal aspect of tarsus.
- Fig. 59. *Chelymorpha argus*, cephalic aspect of mesothoracic leg.
- Fig. 60. *Chlamys plicata*, cephalic aspect of tarsus.
- Fig. 61. *Donacia* sp., cephalic aspect of mesothoracic leg.
- Fig. 62. *Dibolia borealis*, detail of cuticle.
- Fig. 63. *Phyllobrotica discoidea*, detail of cuticle.

Plate V.



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